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Aspects of Spore Dispersal in *Selaginella*

Dedicated to the memory of Prof. Dr. Tadeus Reichstein

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ABSTRACT.—The evolution of heterospory changed the conditions for spore dispersal. Assuming wind as the dispersal agent, microspores will be dispersed to greater distances than megaspores. We investigated aspects of spore size and sculpture as well as spore dispersal under calm conditions and under the effect of artificial wind of some *Selaginella* species. We found that differences between the species existed that were correlated with active or passive release of micro- and megaspores. The dispersal efficacy changed drastically under the effect of wind, showing differences between the species. There was no support for the hypothesis of synaptospory between micro- and megaspores during active dispersal. Evidence suggests that active spore dispersal and wind may enhance outbreeding. More detailed investigations may reveal species specific correlations between life history traits, breeding systems, and spore dispersal.

Heterospory and dioecy of gametophytes evolved independently in different clades of the pteridophytes. The separation of female megaspores and male microspores changed the conditions of spore dispersal. In homosporous, wind dispersed ferns the probability of being transported a certain distance is much the same for each spore. Assuming that in heterosporous pteridophytes wind dispersal is still dominant, the smaller and lighter microspores are likely to be dispersed to longer distances than the larger and heavier megaspores (Tryon and Lugardon, 1991). The dispersal distances of male and female gametophytes thus differ. Heterospory also affects the production of spores. Because of higher energetic investments, the number of megaspores per individual plant is reduced in comparison to the number of microspores (Tryon and Tryon, 1982). As a consequence, the dispersal ecology of heterosporous pteridophytes is likely to differ from that of homosporous ferns (Cousens, 1988).

The heterosporous genus *Selaginella* P. Beauv. is widespread and contains numerous species (Jermy, 1990). The efficacy of their active spore dispersal mechanisms was first investigated by Goebel (1901). He showed that the megasporangium ejects the megaspores in a manner quite different from the microspore release mechanism of the microsporangium (Goebel, 1901). He gave a detailed description of the mechanism of megaspore release that was recently rediscovered by Page (1989). The active megaspore discharge mechanism was termed "compression and slingshot ejection" (Page, 1989). Studies by Straka

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(1962), Somers (1982), and Koller and Scheckler (1986) revealed that variations in release mechanisms of microspores exist. Passive spore release as well as active spore release were found. Both types can occur under conditions of calm or wind. Active spore release is due to sudden movements of the microsporangium walls caused by changes of the cell turgor during desiccation.

A possible function of spore sculpture in respect to dispersal, namely synaptospory, was emphasized by Kramer (1977). Primary synaptospory means that diaspores are dispersed together straight away from the source plant, whereas secondary synaptospory describes the sticking together of diaspores after the dispersal of single spores. Spore sculptures may enhance synaptospory. A special type of synaptospory may be found in heterosporous ferns, i.e., the dispersal of units consisting of micro- and megaspores.

The ecological consequences of the different above-mentioned spore release and dispersal mechanisms have not yet been studied. In the present investigation we compare the spore dispersal of five species of *Selaginella.* We address the following questions: 1) Are there morphological characteristics of the micro- and megasporangia and/or the micro- and megaspores that support dispersal mechanisms? 2) Do the species differ with respect to release modes? 3) Do different release mechanisms of micro- and megaspores result in differences in dispersal distances? 4) How do these distances change under the effect of wind? 5) Does primary synaptospory between micro- and megaspores occur?

Methods and Materials

The Species.—The following species cultivated in the Botanical Garden of the University of Zürich were investigated: *Selaginella anceps* (C. Presl) C. Presl, *S. kraussiana* A. Braun, *S. lepidophylla* Spring, *S. martensii* Spring, and *S. pallescens* (C. Presl) Spring. The species were identified using Vareschi (1968) and Alston et al. (1981).

Morphological Traits of Sporangia and Spores.—The size (largest diameter) and the surface sculpture of the outer spore wall of micro- and megaspores were determined using a light microscope and SEM. Sizes of both spore types were measured roughly; a statistically relevant measurement of spore sizes was not intended. The arrangement of micro- and megasporangia on morphological units of plants (see below) was determined using a dissecting microscope. Sporangial arrangement of each species was assigned to the four types given by Horner and Arnott (1963). Type I: basal megasporangiate zone and superior microsporangiate zone; Type II: two rows of megasporangia and two rows of microsporangia within each strobilus; Type II': strobili with two rows of microsporangia and two rows containing both mega- and microsporangia; Type III: wholly megasporangiate strobili.

Spore Release.—The opening of sporangia and the manner of active and passive spore release were observed visually in all five species under a dissecting

microscope. Micro- and megaspore release in *S. lepidophylla* and *S. martensii* were studied additionally with a video camera fitted with a macro lens.

SPORE DISPERSAL.—Because of the branching morphology of *Selaginella,* we used morphological units of plants as spore sources. These were vertically oriented, frond-like parts of fertile shoots about 40 cm long in *S. anceps, S. martensii,* and *S. pallescens.* The units were short, horizontally oriented shoots of *S. lepidophylla* and short, horizontal parts of shoots with some erect strobili in *S. kraussiana.* As a consequence, the spores were not released at even heights in all experiments. This experimental design was chosen in order to get an impression of the pattern of spore dispersal distances under natural conditions.

We arranged two types of experiments, one in calm and one with moderate wind. Both experiments were carried out in a calm room. Room temperature was constant at 20°C, which allowed slow desiccation of the morphological units, a basic requirement for spore dispersal. The floor of the room was covered with black paper.

Morphological units bearing ripe micro- and megasporangia of *S. anceps, S. martensii,* and *S. pallescens* were placed erectly with the strobili at an approximate height of 30 cm above surface. Eight rows, each of 59 cm length, of microscope slides covered with double-sided clear sticky tape were laid at angles of 45° around the spore source. The experiments were conducted for twelve hours. Then, the diaspores (single microspores, tetrads of microspores or single megaspores) were counted in each centimeter of each row on an area of 16 mm^2 under a light microscope. The numbers of diaspores were extrapolated to 1 cm^2, and the mean per cm distance from the spore source of the eight rows was calculated. For *S. kraussiana* and *S. lepidophylla,* a similar experiment was performed, but because of the much smaller morphological units of these plants (strobili at a height of 3–4 cm above the surface), they were carried out in large plastic boxes, and the 8 rows around the spore source had a length of 14 cm.

We also investigated the spore dispersal of *S. anceps, S. kraussiana,* and *S. martensii* under the influence of wind. Again, morphological units of these species were placed in a calm room. Five rows of microscope slides with double-sided clear sticky tape, each 119 cm long, were laid at angles of 45° in a semicircle on one side of the spore source. On the other side, a small electric propeller (König AG, Zürich, type 316; diameter of the propeller = 19 cm) was placed at a distance of 1 m. This propeller did not produce a linear wind flow, but an air current with turbulence, which we believe to be more representative for natural wind conditions. The wind speed was measured at the position of the strobili using a digital data logger (Squirrel, Grant Ltd., Britain). In all experiments a moderate mean wind speed of 1.16 m/s was adjusted. The experiments again were conducted for twelve hours. Data analysis was carried out in the manner described above.

SYNAPTOSPORY.—All experiments were carefully checked for eventual synaptospory between micro- and megaspores.

TABLE 1. Morphological characteristics of microspores, megaspores, and strobili of *Selaginella anceps, S. kraussiana, S. lepidophylla, S. martensii,* and *S. pallescens* used in dispersal experiments. Arrangement of sporangia within strobili according to Horner and Arnott (1963; for explanations see text).

Species	*Selaginella anceps*	*Selaginella kraussiana*	*Selaginella lepidophylla*	*Selaginella martensii*	*Selaginella pallescens*
Microspore dispersal units, and their size	~ 40 μm tetrads	~ 40 μm singles	~ 50 μm tetrads	~ 40 μm tetrads	~ 30 μm singles or tetrads
Surface of microspores	obtuse cones	spiny	burlike structured	finely prickly	papillate
Size of megaspores	~ 300 μm (with flange)	~ 620 μm	~ 300 μm	~ 380 μm	~ 330 μm
Surface of megaspores	with large equatorial flange	distantly reticulate	feltlike	feltlike	narrowly reticulate
Release of microspores	active	passive	active	active	active
Release of megaspores	passive	active	active	active	active
Arrangement of sporangia within strobili	type I	type I	type II	type I	type II′
Approximative height of sporangia above surface	~ 30 cm within the plane of the shoot	~ 3 cm vertical	~ 3 cm horizontal	~ 25 cm within the plane of the shoot	~ 25 cm within the plane of the shoot

RESULTS

CHARACTERIZATION OF MICRO- AND MEGASPORES.—The investigated species of *Selaginella* had megaspores that were 6–16 times larger in diameter than the dispersal units of the microspores, i.e., single microspores or microspore tetrads (Table 1). The largest megaspores were found in *S. kraussiana* (ca. 620 μm in diameter). In *S. anceps, S. lepidophylla,* and *S. martensii* microspores were dispersed as tetrads (Table 1). *Selaginella kraussiana* dispersed single microspores, whereas in *S. pallescens* both single microspores and tetrads occurred. It is noteworthy that the single microspores of *S. kraussiana* approximately reached the size of the microspore tetrads of the other species.

The surfaces of both types of spores showed distinct characterizations (Table 1, Fig. 1). In *S. anceps,* the megaspores were characterized by a large equatorial flange. The microspores of *S. kraussiana* were extremely spiny. In *S. lepidophylla,* the surfaces of the microspore tetrads had burlike structures at the edges that seemed to be complementary to the feltlike surfaces of the megaspores. A similar case was found in *S. martensii,* but here the microspore tetrads were finely prickly. In two of the investigated species, surface structures of the spores were documented, which principally allowed synaptospory between micro- and megaspores, whereas the surface structures of all five species allowed synaptospory of microspores. In the dispersal experiments (see

below), we sometimes observed groups of microspore tetrads dispersed as one unit.

ARRANGEMENT OF MICRO- AND MEGASPORES WITHIN THE STROBILI.—We found three of the four types of sporangial arrangement described by Horner and Arnott (1963). Type I, with megasporangia at the base of the strobilus, occured in *S. kraussiana, S. martensii,* and *S. anceps.* Type II, with entirely vertical rows of either micro- or megasporangia, was documented in *S. lepidophylla,* and type II', with vertical, but intermingled rows of both sporangial types, was found in *S. pallescens.*

The strobili usually were oriented within the plane of the morphological unit, i.e., the shoot (Table 1). Depending on the architecture of the species, the sporangia were oriented strictly vertically or horizontally, the latter observed in *S. kraussiana,* with tower-like strobili.

SPORE RELEASE.—The height above surface at which the spores were released changed among the species and clearly affected the dispersal distances. The strobili of *S. kraussiana* and *S. lepidophylla* were at heights of only 3 cm above surface (Table 1).

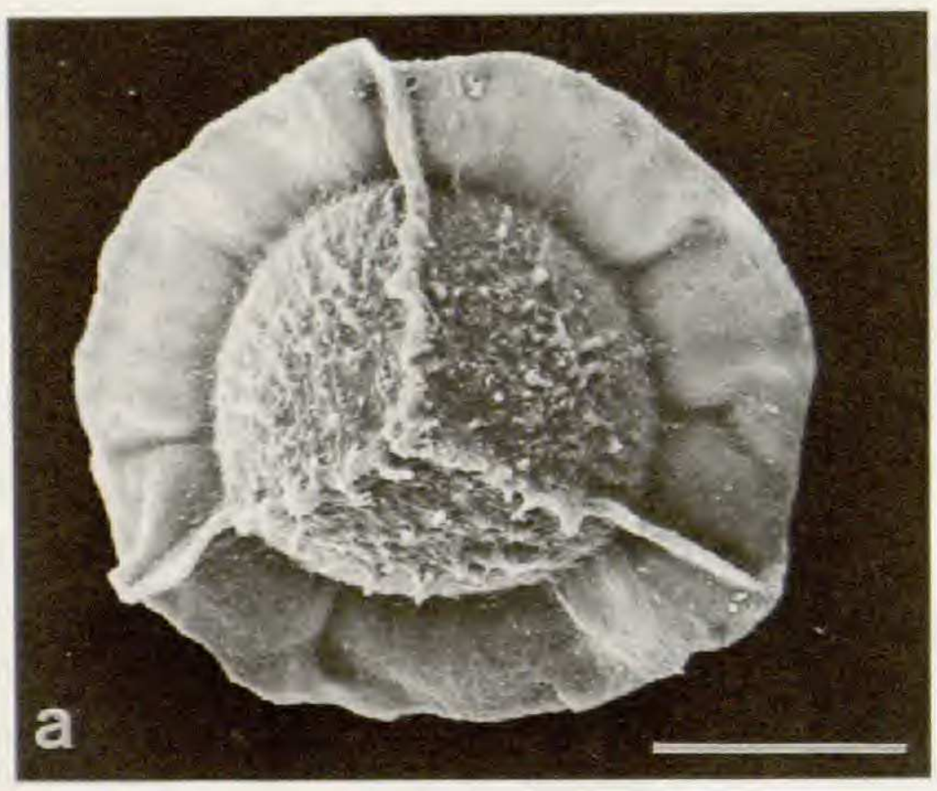
Microspores were either actively or passively dispersed (Table 1). In *S. kraussiana,* the microsporangium opened along a preformed dehiscence line, and the microspores were passively dispersed (as described in Koller and Scheckler, 1986). The two valves of the sporangial wall opened during desiccation. Subsequently, they remained open. The microspores were exposed to the air and, as a consequence, the tapetal secretion on the inner surface of the valves dried. Some spores fell out and some were dispersed by wind.

The microsporangia of the other four species dispersed their spores actively (Table 1). The sporangium started to open at the distal end and continued opening along a preformed dehiscent line. The two valves of the microsporangia spread and their borders bent backwards. When the angle between the valves reached about 150°, the sporangium suddenly closed, actively dispersing the microspores.

In *S. anceps,* the megaspores fell passively out of the open sporangium and were not dispersed by a slingshot mechanism (Table 1). Therefore, in *S. anceps,* only the microspores were actively dispersed.

In the other four investigated species of *Selaginella,* the megasporangium opened in the manner described by Page (1989). During desiccation, the valves spread until an angle of about 150° was reached. The megaspores were then separate from each other. The two outer megaspores, i.e., the ones lying at the borders of the valves, were both located in hollows of the corresponding valves. The two inner megaspores were in the boat-shaped basal part of the sporangium. With a sudden movement, the valves sprang back into their original position, actively ejecting the megaspores (Table 1).

During the opening of the micro- and megasporangia the sporophylls spread to an angle of approximately 90° or even more, leaving space for spore dispersal. After spore release they closed again to an angle of 45°.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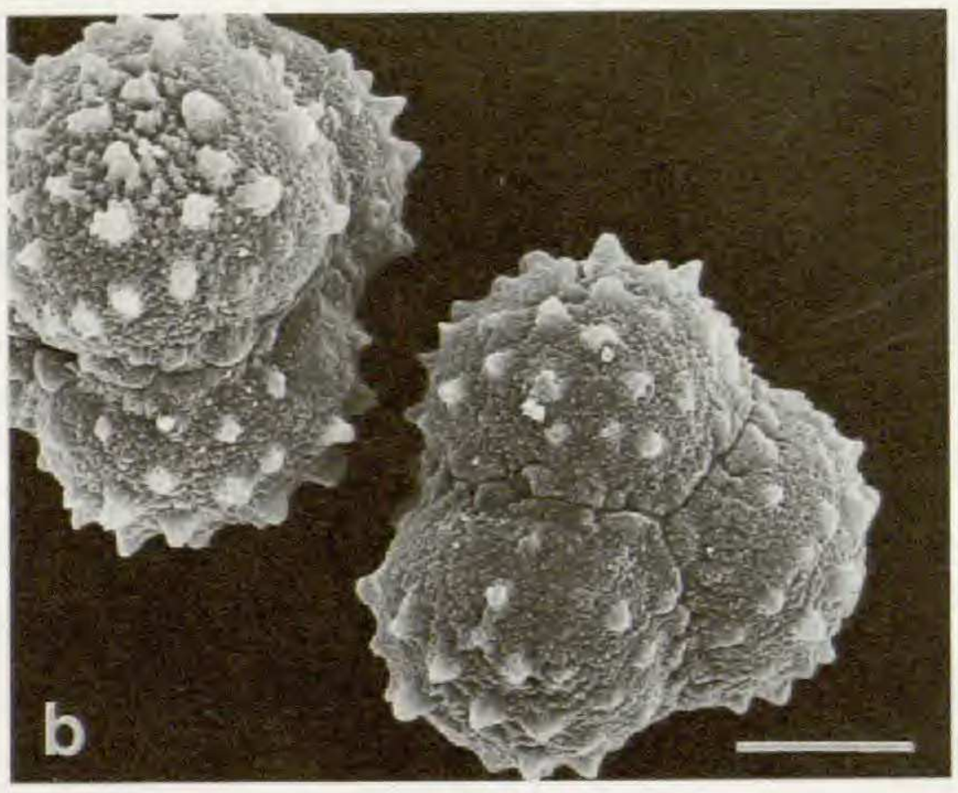
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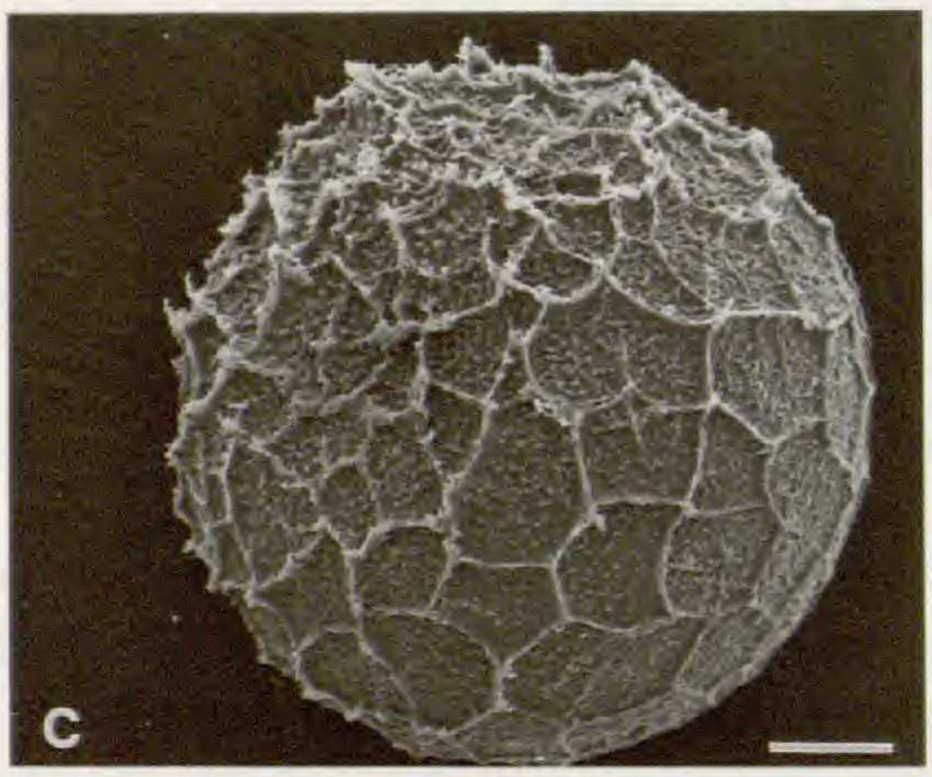
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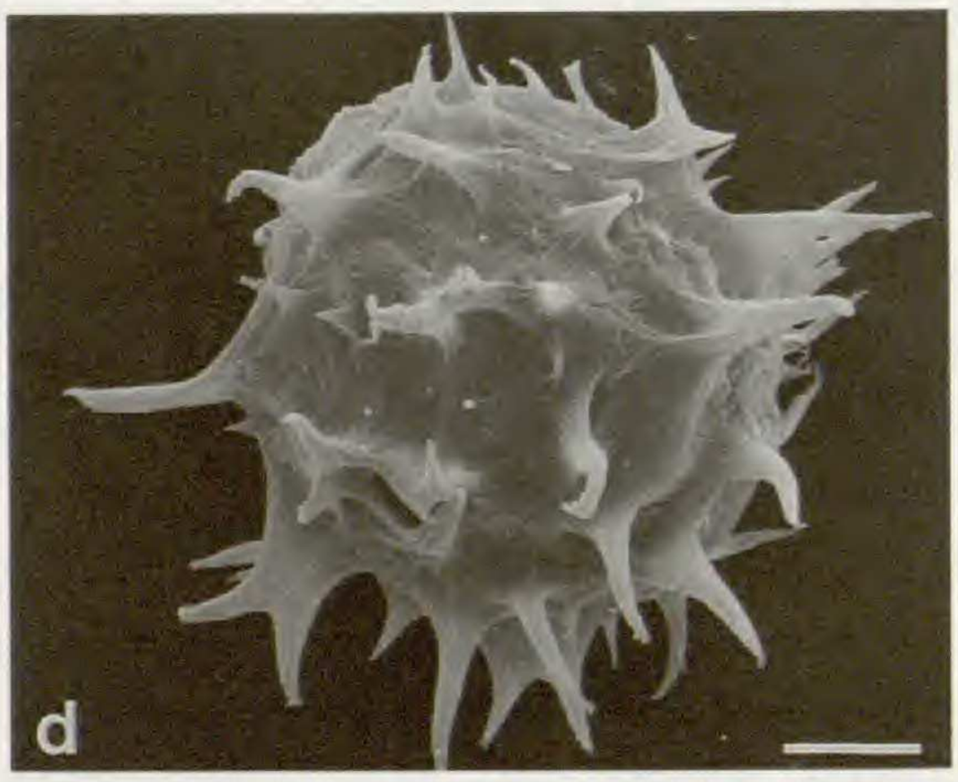
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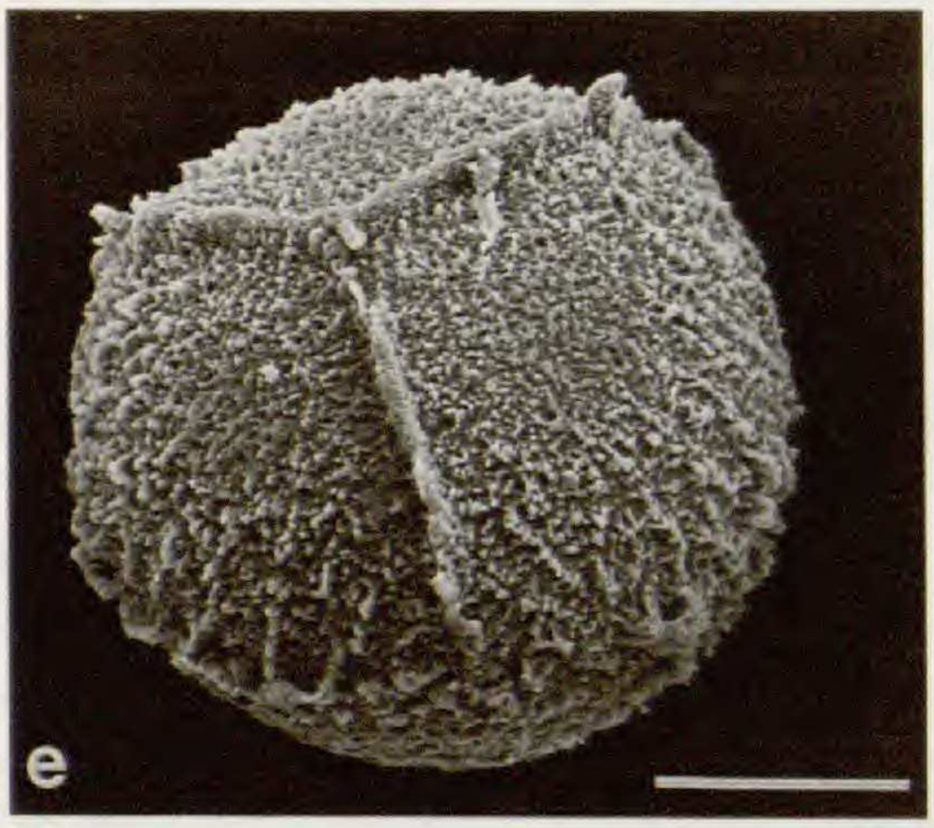
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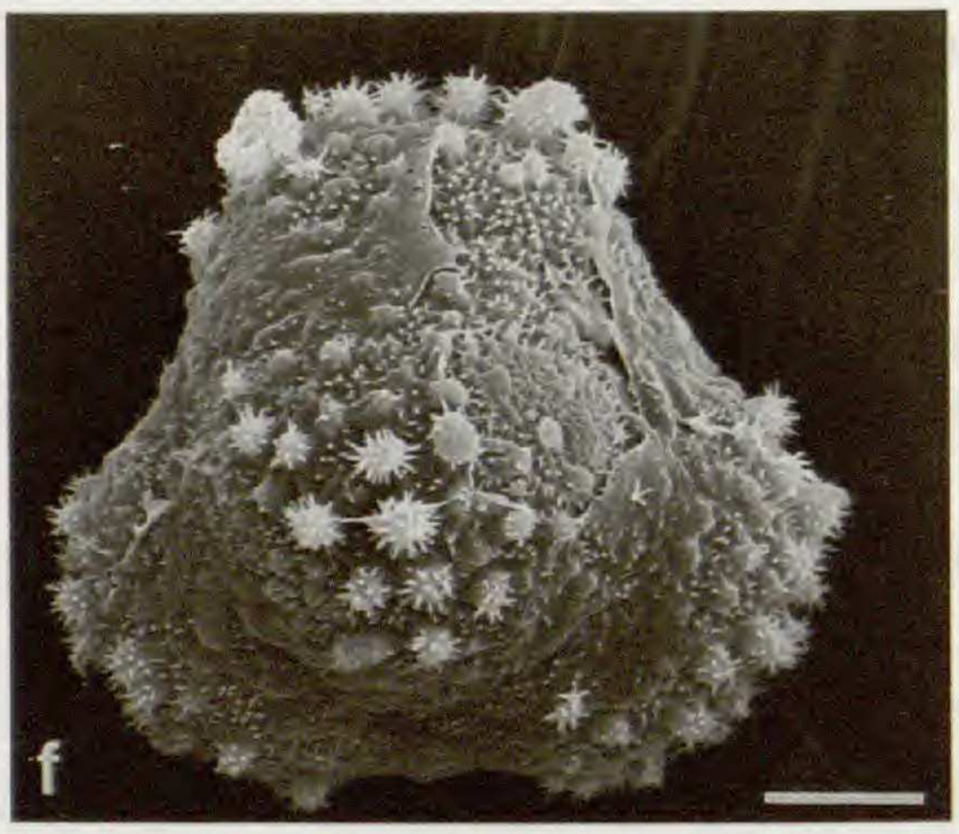
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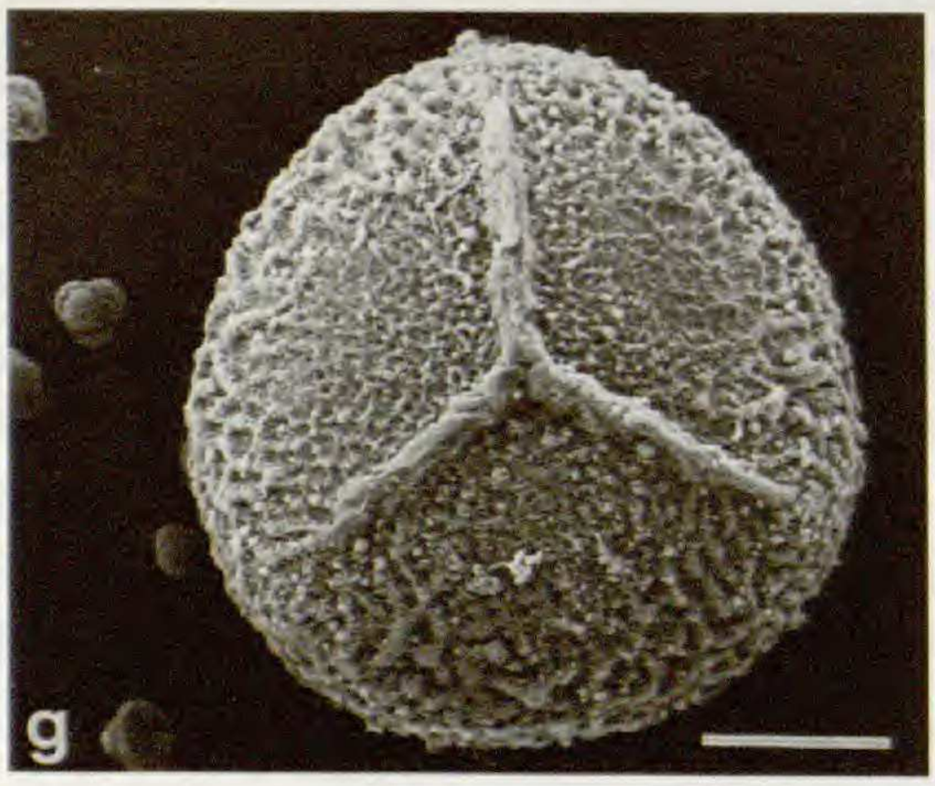
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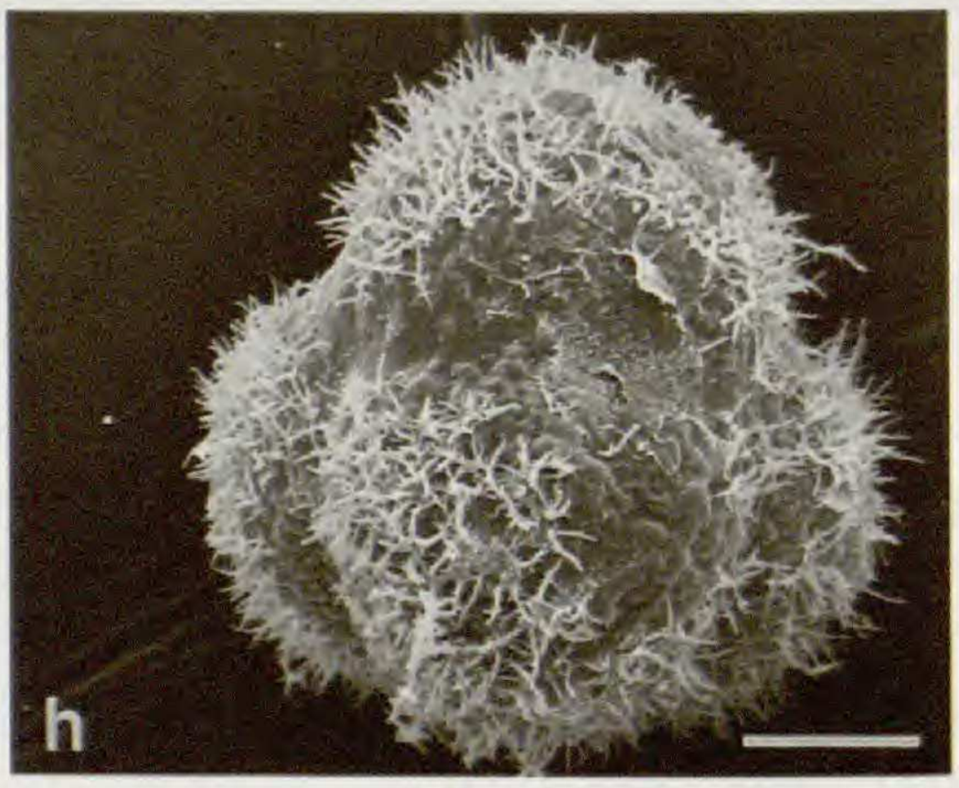
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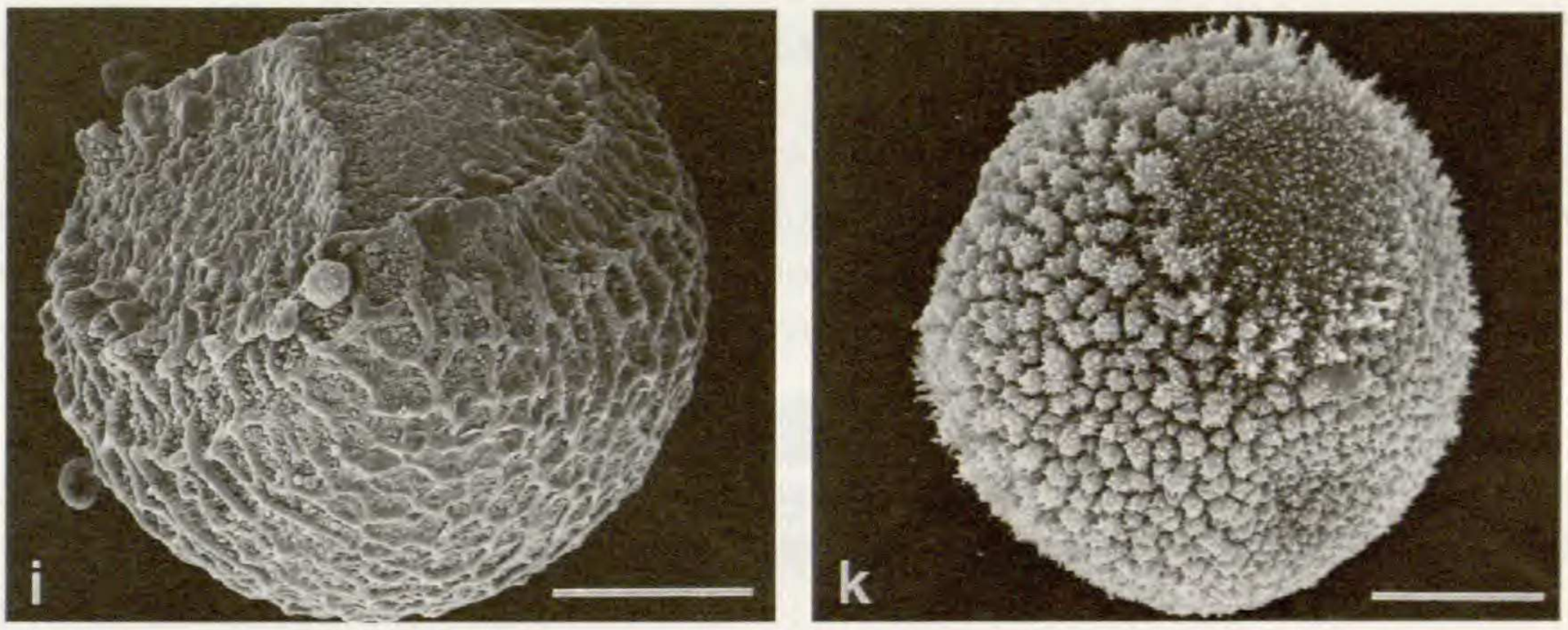

FIG. 1. Continued.

SPORE DISPERSAL.—In *S. anceps,* most megaspores were only dispersed into the close vicinity of the spore source in the experiments without wind (Fig. 2), a result that is in accordance to the passive spore release mechanism of this species. Densities of 1300 microspore tetrads (Fig. 1b) per cm^2 were found within 20 cm from the source (Fig. 2). The majority of the microspores landed here, leading to the well known leptocurtic curve of spore dispersal (Fig. 2). However, a minority was dispersed to distances up to 59 cm. Microspores were often clumped together, forming groups of sometimes up to 100 tetrads. This seemed to be due mainly to a tapetal secretion on the surfaces of the spores. Under the influence of a moderate wind of 1.16 m/s, an almost uniform dispersal curve was observed, exhibiting no obvious peaks (Fig. 2). The abundance of microspores within the range of the experiment decreased only slightly with increasing distance from the source. The megaspores also reached greater distances—up to 69 cm in the experiment with wind—possibly assisted by their large equatorial flange (Fig. 1a).

Similar results were obtained for the microspore tetrads in the experiments with *S. martensii* (Fig. 2). Near the spore source, we counted about 920 microspore tetrads per cm^2. In marked contrast to *S. anceps,* the actively released megaspores of *S. martensii* reached similar distances in calm conditions and under the effect of wind (Fig. 2), i.e., up to 59 cm from the spore source. Under calm conditions in the experiment with *S. pallescens* (Fig. 2), the results of micro- and megaspores corresponded to the dispersal curves found in *S. martensii* (Fig. 2).

Selaginella lepidophylla and *S. kraussiana* differed from the above de-

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FIG. 1. SEM micrographs of microspores and megaspores of *Selaginella* species. a) proximal view of a megaspore of *S. anceps* with equatorial flange; b) microspore tetrads of *S. anceps*; c) equatorial view of a megaspore of *S. kraussiana*; d) single, spiny microspore of *S. kraussiana*; e) proximal view of a megaspore of *S. lepidophylla*; f) microspore tetrad of *S. lepidophylla*; g) proximal view of a megaspore of *S. martensii*; h) finely prickly microspore tetrad of *S. martensii*; i) equatorial view of a megaspore of *S. pallescens*; k) single microspore of *S. pallescens*. Scale bars: a, c, e, g, i = 100 μm; b, d, f, h, k = 10μm.

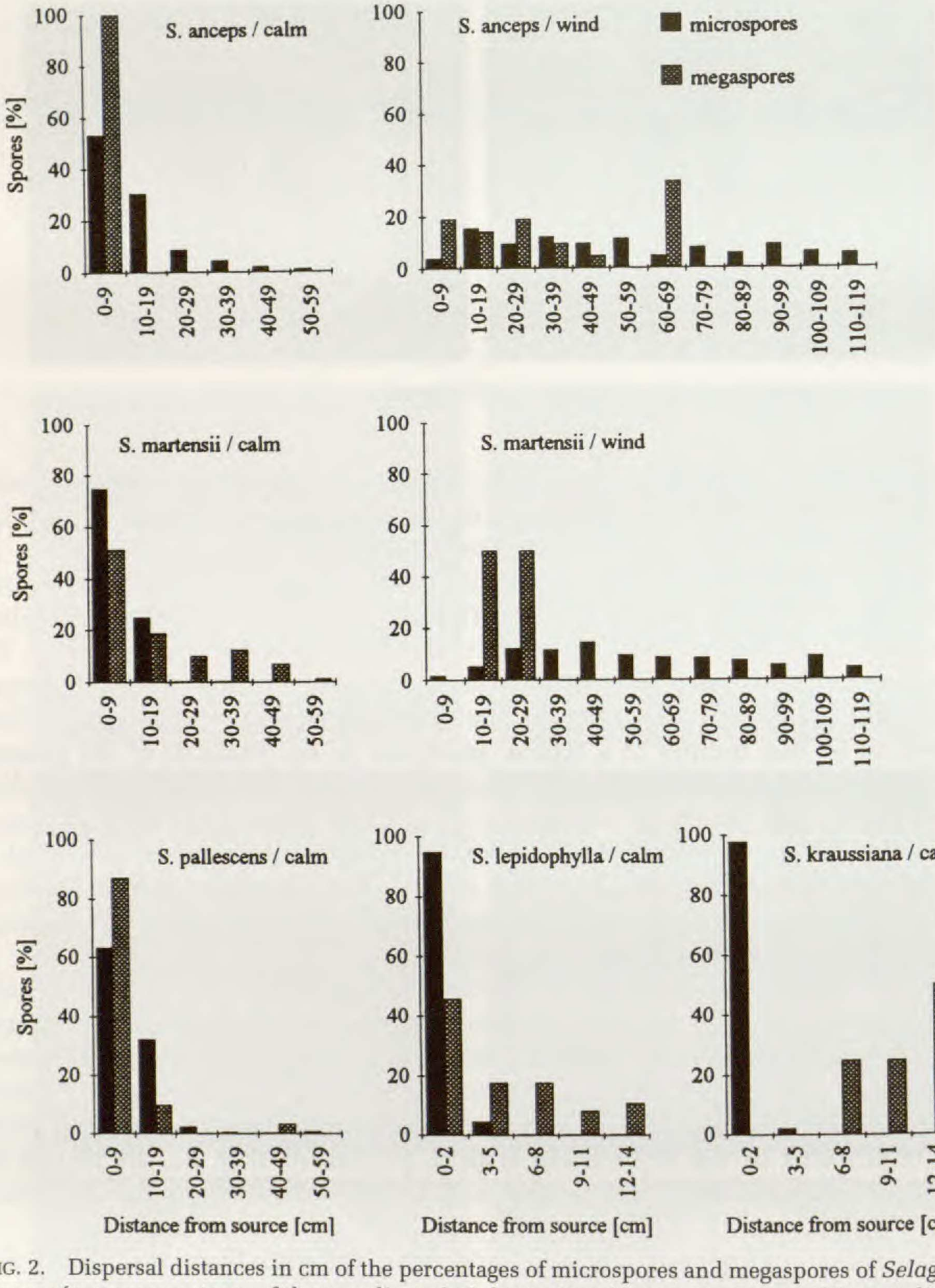

FIG. 2. Dispersal distances in cm of the percentages of microspores and megaspores of *Selaginella anceps* (mean percentages of three replicates), *S. kraussiana* (mean percentages of four replicates), *S. lepidophylla* (mean percentages of three replicates), *S. pallescens*, and *S. martensii* in calm or with wind (1.16 m/s). Note different scales of the x-axis.

scribed species in the height of strobili above ground, which was only about 3–4 cm (Table 1). The actively dispersed megaspores of both species reached distances of at least 14 cm under calm conditions, but most of the microspore tetrads in *S. lepidophylla* (Fig. 2), and most of the spiny single spores in *S.*

kraussiana were found close to the spore source (up to 2 cm; Fig. 2). In an experiment with wind, only a few micro- and megaspores were found in *S. kraussiana* and the results are therefore not shown. Because there were ripe sporangia of both types on the morphological units and because these sporangia were obviously empty after the experiment, one had to conclude that the spiny microspores were dispersed for much greater distances than the 119 cm of the experimental setup.

SYNAPTOSPORY.—In all investigations as well as in the dispersal experiments no case of primary synaptospory between micro- and megaspores was detected.

DISCUSSION

In homosporous ferns a single viable spore is theoretically sufficient to achieve a new sporophyte and to found a new population, due to intragametophytic selfing (Schneller and Holderegger, 1996). In any heterosporous species a microspore and a megaspore must be placed in close proximity to generate a new sporophyte (Kramer, 1977). The formation of heavy megaspores, compared with small, light microspores, clearly reduces the effectiveness of wind dispersal, and thus the potential for long distance dispersal. As a consequence, the dispersal units of heterosporous pteridophytes differ in primary dispersal distances: the microspores have the ability to be dispersed for long distances, whereas the megaspores are dispersed only locally.

Heterospory ultimately led to the differentiation of two types of sporangia. Earlier investigations (Goebel, 1901; Steinbrinck, 1902; Somers, 1982; Koller & Scheckler, 1986; Page, 1989) revealed the morphological, anatomical, and functional differences between micro- and megasporangia in the genus *Selaginella*. The five species of *Selaginella* investigated in the present study also exhibited marked differences in the manner of spore release. Schneller (1995) showed that differences in spore release also occur between homosporous ferns.

As hypothesized by Kramer (1977), primary synaptospory (as well as secondary) of mega- and microspores could be a mechanism to assure fertilization in heterosporous pteridophytes. If this is the case, the genetic variation within the progeny would consequently be restricted due to intergametophytic selfing. Kramer (1977) and Dahlen (1990) gave some morphological evidence in favor of this hypothesis. The surface structures of micro- and megaspores often seem to fit together in a lock and key manner. In our investigations, we also detected some morphological characteristics of the spore surfaces that suggested synaptospory. Microspores would then "ride" on ejected megaspores. However, this hypothesis of synaptospory between micro- and megaspores could not be confirmed in our investigations. Mega- and microspores were dispersed separately.

To our knowledge, no investigations exist on spore dispersal of *Selaginella* under natural conditions. Published data on dispersal distances (Mitchell,

1910; Ingold, 1939; Page, 1989) are based on laboratory observations under calm conditions. In our experiments using artificial wind, we showed that the microspores are easily transported and well spread over distances of more than 1 m from the spore source. Compared to the mean size of the spores of homosporous ferns (Kramer et al., 1995), the microspores of *Selaginella* species are smaller and thus more effectively wind dispersed. Wind also seems to have effects on megaspore dispersal (Fig. 2), especially in the case of the passively dispersed megaspores of *S. anceps,* which are characterized by a large equatorial flange. In nature, microspores would disperse far greater distances than megaspores under the influence of wind, turbulence, and squalls. Long distance dispersal of microspores thus increases the probability for outbreeding. Active mechanical dispersal and wind dispersal are not mutually exclusive. The former can additionally faciliate wind dispersal. Active spore release by the megasporangium would further enhance the possibility of cross fertilization, especially in calm, when the majority of microspores are deposited adjacent to the source (leptocurtic dispersal curve; Fig. 2) and the megaspores are dispersed greater distances. This effective active megaspore release mechanism may also increase the probability for the establishment of new sporophytes due to decreased competition among siblings.

Secondary synaptospory after spore dispersal may be relevant in promoting fertilization. The complementary spore surface sculptures of micro- and megaspores possibly play a role in the effectiveness of secondary synaptospory. A group of fertile microspores or a group of microspore tetrads in the vicinity of a megaprothallium may significantly enhance the probability of fertilization, because of its higher number of spermatozoids that are released. Water and electrostatic effects may also play a role in secondary synaptospory.

We do not know much about the breeding systems of *Selaginella* species, especially in natural populations. Simple breeding experiments showed that *S. martensii* frequently formed viable sporophytes through intergametophytic selfing (Filippini-De Giorgi, unpubl. data). In an electrophoretic study of some populations of *S. helvetica* in Switzerland, considerable genetic variation within and among populations was found (Holderegger and Schneller, unpubl. data). We believe that dispersal is an important but unfortunately neglected part of the life cycle in studies of population biology of pteridophytes. Our preliminary study on the dispersal biology of heterosporous *Selaginella* species reveals many possible correlations between morphology, surface sculpture of the outer spore wall, ecological determinants like drought or wind, breeding system, and population genetics. Further, thorough studies should include the determination of the terminal settling velocities of either spore type (see Niklas, 1992) or experimental designs that allow an investigation of lateral dispersal out from a real point-source (i.e., a single strobilus). The data gathered in our experiments had low statistical power. Therefore, large sample size experiments of spore dispersal under strictly controlled conditions, perhaps in a wind tunnel, are needed. Investigations of additional species using different methods may reveal whether inbreeding and outbreeding occur in natural populations, whether differences in the breeding system between species exist,

and whether these life history traits correlate with the dispersal mode of the species.

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